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HIGH AND LOW LETHAL TEMPERATURES FOR THE WESTERN PINE BEETLE[1]

Introduction

The fact that wood borers and bark beetles may be killed as a result of the heat absorbed by the dead host plant when exposed to sunlight has been known for a number of years. The first published observations of solar heat as lethal to forest insects were made in 1917 by F.C. Craighead[2], who found that the larvae of a cerambycid borer, Cyllene pictus, were killed when infested logs were exposed to the sun. In 1919 and 1920 experiments carried out by J.E. Patterson and the writer in Oregon and California proved the effectiveness of solar heat in producing killing temperatures in yellow pine bark infested by broods of the western pine beetle, Dendroctonus brevicomis Lec. It was found that complete mortality resulted when bark temperatures reached 120° F., and that bark removed from the tree and placed in sunlight reached this and even higher ppints when the air temperatures in the shade ranged from 85 to 90° F.

On the other hand, extreme cold may likewise result in the killing of bark-beetle broods. For example, in December, 1924, unusual low minimum temperatures of from -20° to -25° F. were recorded in the vicinity of Bend, Oreg. Following this cold spell, Mr. A.J. Jaenicke of the Forest Service found that a high percentage of the overwintering larvae were dead over a considerable area of yellow pine infested by the western pine beetle. This mortality, which varied from 25 to 80 per cent, could be accounted for only as a result of freezing of the larvae in the outer bark.

During the winter of 1926-27, at Asheville, N.C., Beal[1] found that general and heavy mortality pf the southern pine beetle, Dendroctonus frontalis Zimm., occurred within a few days after the first severe cold in January. Hopkins[3] attributed the sudden decline of an epidemic of this same beetle in West Virginia to the severe freeze in the winter of 1892-93.

A general treatment of the subject of weather and climate in their relation to insects has recently been published by Uvarov[9]. Other workers in this field have gone more minutely into the effects of low temperatures within the body of the insect itself. Robinson[7,8] has developed a method for determining the natural undercooling and freezing points in insects. This same individual has also shown the water-binding capacity of colloids to be a definite factor in winter hardiness of insects. Several papers by Payne[4,5,6] also deal with the factors involved in the cold-hardiness of insects.

The effects of temperatures on the brood stages of the western pine beetle have been studied since 1920 under both field and laboratory conditions by the Forest Insect Division of the Bureau of Entomology. Laboratory experiments were conducted at Stanford University, Calif., and field studies were located at points in California, Oregon and Idaho. The object of these studies was to determine (1) the high-temperature points which result in mortality in connection with the use of the solar-heat

method of control, and (2) the low-temperature points which result in killing the overwintering brood stages when severe cold weather occurs in infested areas.

The results of these studies, as far as they had advanced at the end of 1929, are presented in this paper.

Material Selected for Study

The material which has been used for testing the effect of temperature has consisted mainly of sections of yellow pine bark infested by the various brood stages of the western pine beetle. The term "brood" is used to designate the progeny of a pair of parent beetles during the period of development within the tree. As used throughout this paper, this term applies to eggs, larvae, pupae and new adults as they are found collectively in the bark samples.

Infested bark was selected as the medium in which exposures were made to extreme temperatures because of the fact that this is the part of the tree which must be treated in the use of the solar-heat method of control, and because the broods which are in overwintering stages in the outer bark are most likely to be subjected to freezing weather temperatures. In infested trees all brood stages except eggs and young larvae are found only in the outer bark. This can be best understood if we consider briefly the life history of the beetle.

Trees are attacked during the active period in late spring, summer and early fall by the parent adults, which make winding tunnels through the live cambium and deposit eggs in notches cut along the sides of these tunnels. After the eggs hatch the young larvae feed for a time in the cambium and inner bark, then bore directly into the corky layers of the outer bark, where they complete their development. Each larva cuts in the outer bark the individual feeding gallery and the cell in which it transforms first to pupa, then to new adult. Consequently any temperatures affecting the larvae and later stages must reach the insect through the protective covering of the outer bark. The cambium and bark contain the primary infestation from the time the tree is attacked until it is eventually abandoned by the new adult beetles. However, the bark is the part of the tree in which the broods will befound during both the midsummer and midwinter periods, when lethal temperatures occur.

In determining the effects of both high and low temperatures, the temperature of outer bark, as recorded by imbedded thermometers, has been used as a basis for correlation with mortality of broods (Fig.1). Records have also been secured of the effect of air temperatures on larvae, pupae and adults exposed in open containers after removal from the bark.

Fig. 1.--Section of infested western yellow pine bark, showing position of thermometer used in recordingtemperatures.

a. Egg galleries of western pine beetle on inner surface of bark;
b. Mines of young larvae in inner bark;
c. Mines of advanced larvae and pupal cells in outer bark;
d. Mercurial thermometer with bulb imbedded at depth of pupal cells and calibrated scale extending beyond bark.

Mortality Resulting from Exposure of Infested Bark to Solar Heat

In experiments with solar heat as a lethal agent there is no means of controlling the degree of heat to which the bark is exposed, as this is dependent entirely upon weather conditions. It is obvious that the only course open to the experimenter is to record the temperatures developed within the bark and compare these with the resultant mortality of the broods. However, the degree of heat that is absorbed by the bark varies decidedly with the angle at which the bark is tipped toward the sun. The maximum is reached during the middle of the day, with the bark placed as nearly as possible with its surface at a 90° angle to the sun's rays. On a standing tree the bark surface of the main trunk is vertical, and therefore nearly parallel to the angle of sun rays at midday during the summer season. This position, together with the contact of the bark on the sapwood, results in conditions which keep bark temperatures well below those producing mortality, even though infested bark on the lower trunk may be exposed to the sun at midday.

This point is illustrated by Fig. 2, which is a chart based upon records taken under forest conditions near Ashland, Oreg., February 11,1920. An infested tree was selected and thermometers were placed as follows: one weather thermometer suspended in shade, about ten feet from tree, to record air temperature; one mercurial stirring-rod thermometer imbedded in infested bark on north side of tree 5 feet above base; one mercurial stirring-rod thermometer imbedded in infested bark on south side of tree 5 feet above base; and one mercurial stirring-rod thermometer imbedded in an infested bark section (12 by 24 inches) removed from tree and placed on ground at base, inner surface upward, in position approximately at a 90° angle of sun rays at midday.

Fig. 2.--Comparative temperatures of infested bark under different exposures, Feb. 11, 1920.

Readings from all four thermometers were taken at 15-minute intervals from 9 a.m. until 3:15 p.m. The entire day remained clear, but shadows from nearby trees caused periods of shade from 9:55 to 10:32 a.m. and from 2 p.m. until sundown.

The readings show that the temperature of the bark section on the ground climbed rapidly when exposed to the sun until 1:30 p.m., when it reached a maximum of 104° F., or 38 degrees higher than the corresponding air temperature. After 1:30 p.m. the temperature of the bark section declined slowly until 2 p.m., and when the shade came on it cooled rapidly during the next hour.

The bark exposed to the sun on the south side of the tree did not become much warmer than air temperature until after 12 m. It reached a maximum of 74° at 2 p.m., or 8 degrees higher than the air temperature at 1:30 p.m. It did not begin to cool until 2 p.m.

Bark temperatures on the north side of the tree lagged well below those of the air and the bark on the south side throughout the period of sunlight. After 2 p.m., as the air temperature cooled the bark attached to the tree retained its heat, and both north and south sides were warmer than air temperature at 3:15 p.m.

This experiment indicates that infested bark attached to a standing tree does not become more than 10° warmer than the corresponding air temperature in the shade, and that it is necessary to remove infested bark and expose it flat on the ground in order that it may absorb sufficient heat to insure higher temperatures.

During the summer of 1920 experiments were conducted to determine what bark temperatures are necessary to produce effective mortality of the western pine beetle and the conditions which are essential in order to produce these lethal temperatures by solar heat. Three tests were carried out by J.E. Patterson at Pinehurst, in southern Oregon, while five tests were made by the writer at Northfork in central California. The months of June, July and August were selected for these tests, as this is the period when, because of fire hazard, it is desirable tomtreat the summer broods by the solar-heat method rather than by burning.

The method used in running these tests was as follows:

1. A series of from 10 to 20 sections of infested bark, 12x24 inches, were taken from the tree early in the morning and spread upon the ground where they would be in sunlight from 10 a.m. to 3 p.m.
2. Thermometers were imbedded in two sections, and readings were taken at 15 or 30 minute intervals throughout the period of exposure.
3. A thermograph was set up within a few yards of the place where the bark was exposed, which recorded at the same intervals the air temperature in the shade.
4. At each interval when temperatures were recorded a bark section was taken from the series exposed on the ground and placed in the shade, where it remained under ordinary air temperatures until broken up in order to count live and dead individuals of the broods.
5. Mortality was determined several days after exposure by breaking and shaving the bark sections so as to expose the broods and count the number of live and dead individuals found.

Table 1 is a summary of one of these tests at Northfork, Calif., June 23, 1920. Temperatures of the two bark sections in which thermometers were imbedded are shown, together with the corresponding air temperatures in the shade. The mortality found afterward in the bark sections at the time readings were taken is also shown. It should be noted that the two bark sections in which thermometers were imbedded did not warm up or cool down at the same rate, nor did they reach the same maximum. However, they were at all times within 8° of each other. The temperature of the bark section removed at time of reading may have differed to this extent from those in which thermometers were placed. These differences can be explained as due to varying thicknesses of bark, slight differendes in "tilt" or angle of exposure, and varying air movements around bark sections. It is altogether probable that the bark section removed at 10 a.m., in which a mortality of 34.3% was found, exceeded by a few degrees the temperatures of 99 and 100° recorded by the imbedded thermometers in other sections. Uniformity of bark temperatures could not be expected under the conditions of the experiment, the main purpose being to determine under what air temperatures the bark would absorb enough heat to compensate for all these variations, so as to secure killing of a high percentage of the broods. The outstanding points shown by this test are that, with air temperature around 80°, the infested bark by 11:30 a.m. had absorbed enough heat to exceed 120° F., and that all bark sections removed after this time showed a mortality of 100%. The maximum spread between bark and air temperatures was at 1:30 p.m., when the bark was approximately 50° warmer than the air.

TABLE 1.--Comparative temperatures in sections of infested bark exposed to sunlight, concurrent air temperatures and subsequent mortality of western pine beetle broods. Northfork, Calif., June 23, 1920

Time	Air Temperature in Shade	Relative Atmospheric Humidity	Temperature recorded in bark section by imbedded thermometer		Condition of western pine beetle larvae and pupae in bark section removed from sunlight (examined July 7, 1920)			
		° F.	Sec. No.1	Sec.No.2	Alive	Dead	Percentage of mortality	
9:30 a.m.	78	25	76	76	150	2	1.3	check
10:00 "	80	25	99	100	96	50	34.3	
10:30 "	79	28	117	109	31	114	78.6	
11:00 "	80	28	122	118	11	186	94.4	
11:30 "	79	28	122	120	0	186	100.	
12:00 M	80	28	124	124	0	185	100.	
12:30 p.m.	81	25	128	128	0	153	100.	
12:55 "	81	25	128	128	0	239	100:	
1:30 "	81	20	132	128	0	227	100.	
2:10 "	84	14	132	126	0	250	100.	
3:00 "	83	12	128	122	0	309	100.	

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The conditions of other tests were varied as to weather conditions and the periodand angle of exposure of bark to the sun's rays. In general it was found that bark removed from the log and placed on the ground at an angle of from 60 to 90° to the sun's rays during midday reached temperatures of from 110 to 132° F. when corresponding air temperatures in the shade ranged from 80 to 95° F.

The results of these studies warrant the following general conclusiona:

1. No mortality due to heat after brief exposures results in bark temperatures do not exceed 100° F.
2. A mortality of 40 to 90% results after several days of exposure when bark temperatures reach maxima ranging from 100 to 115° F.
3. A 100% mortality results from an exposure of 2 or 3 hours when bark temperatures reach a maximum of 115 to 118° F.
4. A 100% mortality results from brief exposures of approximately one hour when bark temperatures reach 120° F. or higher.

In these sixx tests the brood stages ranged from half-grown to full-grown larvae, with a small percentage of pupae and new adults. No attempt was made to separate the resistance of different brood stages to high temperatures, but in these tests it was apparent that pupae and adults are killed by the same high temperaturds that are fatal to the larvae.

In these solar heat tests the factor of relative atmospheric humidity was not isolated from that of temperature. The amount of moisture in the bark is apparently the determining factor in the humidity of the environment of advanced brood stages. After bark is removed from a tree and exposed to the sun a drying-out process takes place, and as the amount of evaporation is reduced the rate at which the bark warms up to high temperatures may be accelerated. This angle of the matter has not been studied, but in the general practice of the solar-heat method of control it has been found that after two or three days the killing of the broods is more effective than during the first day of exposure.

Mortality of Larvae When Exposed to Warm Air Temperatures

As it is impossible to observe the behavior of larvae or other brood stages when exposed in the bark to critical temperatures, a series of laboratory tests was carried out with half- to full-grown larvae removed from the bark and exposed to varying air temperatures. In one test, conditions permitting free evaporation were secured by exposing the larvae to currents of warm air in circulation. As a contrast, conditions in which evaporation was reduced to a minimum were secured by sealing the larvae in glass vials and submerging these under water, which was then slowly heated through the range of critical temperatures. The results of these tests are shown in Table 2.

Table 2--Effect of warm air temperatures on larvae removed from bark

Temperature ° F.	Lot 1: 100 larvae in 5 groups of 20 each in open pasteboard containers; these were exposed at varying heights over an electric plate, permitting free air circulation and evaporation	Lot 2: 100 larvae in 5 groups of 20 each in glass vials sealed with paraffin. These vials were submerged in water which was slowly heated through the range of temperatures indicated
70 to 90	Normally active	Normally active
90 " 95	Maximum activity	Maximum activity
95 " 100	Slight activity; paralysis after prolonged exposure	Activity decreases
100 " 105	Paralysis after brief exposure; complete mortality after 30 min. exp. at 105°	Slight activity continues up to 105°
105 " 110	Fatal after brief exposure	Paralysis of larvae occurs after long exp. (several hours) at 108-110°; larvae recover if retd. to normal temperatures
110 " 115	Fatal after brief exposure	Paralysis occurs after 20 min. exp.; larvae donot recover if retd. to normal temps.
115 " 120	Fatal after brief exposure	Complete mortality occurs after long exp. bet. 115 and 118°; no larvae survive even brief exp. above 118°

Larvae in sealed containers were killed within the same approximate range of temperatures as those in the outer bark. However, in the open-air containers which permitted free evaporation the critical temperatures were 5-8° lower and mortality was practically complete at 110° F.

The condition termed paralysis was also observed in certain larvae removed from the bark after solar-heat tests. When it occurs all movement of the insect ceases and it fails to respond to a stimulus such as the touch of a camel's-hair brush. The larvae donnot, howver, take on the discolored appearance which develops within a day or so after they have been killed. Paralyzed larvae may recover and continue their development if the temperatures producing this condition are not too prolonged. In Lot 2 some of the larvae which were paralyzed at 115° remained in this dormant condition for several months, but eventually assumed the characteristic color of dead larvae and did not recover.

Character of Freezing Experiments and Equipment

During the winters of 1926-27, 1927-28 and 1928-29 a series of tests were carried out by the Bur.Ent. Laboratory at Stanford Univ., Calif., to determine the freezing temperatures fatal to the western pine beetle. As in the solar-heat tests, bark temperatures were recorded by imbedded mercurial thermometers. The apparatus used to determine bark temperatures at the depth of the infesting broods is shown in Fig. 1. The entire calibrated scale used on the glass-rod thermometer extends outside the bark, so that it is possible to take readings without disturbing the bulb.

Low temperatures were controlled by the use of a specially-designed tank cabinet with a carbon-bisulphide compressing unit. This outfit provided two 10x16x24" air compartments in an insulated brine tank, which contained a compressing coil operated by a one-third-horsepower motor. The two freezing compartments opened at the top and were covered with insulated lids. Air temperatures as low as -24° F. were obtainable in the compartments used as containers for infested bark. Bark and air temperatures wereread when the cover was removed, the operation requiring less than 30 seconds. This obviated the use of thermocouples, which would have been of little advantage, since in nearly all experiments it was necessary to open the cabinet at each reading in order to take out an infested bark section. Owing to bark thickness little change in its temperature occurred during the brief interval while readings were taken.

Sections of about 2 sq.ft. each of infested bark were used as units in these freezing tests. Each test, which included a group of 6 to 10 sections, was started with temperatures in the compartments slightly below that of the laboratory and then lowered until the bark temperatures had reached the desired minimum. At determined intervals bark sections were removed from the compartment and kept in the laboratory under normal room temperatures. After 24 hours or more the bark was broken up, the brood removed, and a count made of live and dead individuals. In doubtful cases the brood was kept under observation for several days or longer until dead individuals would be distinguished by discoloration from dormant ones which were recovering.

Fig. 3 is a photograph comparing live and dead larvae removed from bark after exposure to a temperature of -5° F. Larvae killed by freezing have a characteristic blackened appearance which readily distinguishes them from those which survive.

Fig. 3--Larvae of w.p.b. removed from bark 2 days after exposure to a temperature of -5° F.

A. 23 living larvae which survived; theseare normal in color and active when disturbed; when not in motion they usually lie in a curled position with head and anal end turned toward ventral surface of body.

B. 32 dead larvae; these are discolored and show no activity; the body tissues are soft and the larvae usually lie in a distended position.

The material used was secured from two regional areas representing different climatic conditions. The greater part came from infested trees near Northfork, Calif., where winters are mild and minimum temperatures seldom fall below 10° F. A smaller quantity of material was secured from Coeur d'Alene, where winter temperatures occasionally fall as low as -20° F.

Effects on Larvae Under Varying Conditions of Exposure

The method of exposure to low temperatures in the freezing cabinet was varied, first as to the time in which bark was cooled from normal to subzero temperatures, and second as to the condition of the brood--whether dormant or active. The time during which the bark was allowed to warm back from subzero to normal stages was also varied, but it was soon found that this did not affect the resultant mortality after fatal low temperatures had once been reached.

The results obtained from five differently treated groups of bark sections from the material collected at Northfork are summarized in Table 2. In some of this material a mortality of 1-3% of the advanced larvae had already occurred in the field at the time the bark was collected, due in part to parasites and to other causes not determined. However, the low mortality from natural causes did not materially affect the results of freezing. Mortality considerably in excess of that found under normal conditions resulted even at the first critical temperatures between 5 and 0° F.

Results shown in Table 3 indicate that, regardless of the variables introduced by differences in rate of cooling and in condition of the broods, mortality of the larvae due to cold appears between 5 and 0° F.; mortality exceeds 50% at -5° and is practically complete at -10°. A diagram of temperatures and corresponding mortality for Lot 1 is shown in Fig. 4.

In Lot 5 an effort was made to simulate the daily range of temperatures in the field, where cold nights and warm days are a feature of fall weather conditions when the broods are preparing for the overwintering period. The possibility that short periods of cold producing dormancy with intervening periods permitting activity might enable the broods to undergo a hardening process and withstand much lower temperatures than if suddenly exposed to critical temperatures was considered in planning this test.

Table 3.--Effects of low temperatures on larvae of the w.p.b. under varying conditions of exposure, 1928

Lot No. and conditions of experiment	Bark Section No.	Removed from cabinet: Date	Removed from cabinet: Hour	Bark temp. when removed: °F.	Date of Examination	Number of Larvae: Alive	Number of Larvae: Dead	Percent. of Mortality
Lot.1.-Bark tf:								
from field and:	Check	Jan.	4:11:30 a.m.	46	Jan. 7:	185	0	0
placed in cab-:	No. 1		4: 2:15 p.m.	25		5: 23	0	0
inet after	2		4: 3:25 "	20		5: 11	0	0
short period	3		4: 4:30 "	15		5: 43	0	0
in laboratory;:	4		4: 6;00 "	10		6: 135	0	0
temperature	5		4 :7:45 "	5		6: 27	0	0
lowered from	6		4: 9:45 "	0		6: 148	33	18.2
45 to -18°	7		5:10:45 a.m.	-5		6-18: 53	150	73.8
within 48 hrs.:	7		5:12:45 p.m.	-10		6-18: 7	248	97
	8		5: 4:25 "	-15		6,19: 0	168	100
	9		6: 8:40 a.m.	-18		6,19: 0	181	100
	10		8: 4:00 p.m.	+26		19: 0	97	100
Lot 2.--Bark	Check	Jan.	11:10:30 a.m.	48	Jan.	13: 100	0	0
transferred	1		12:12:30 p.m.	20		13: 100	0	0
from field and:	2		13: 4:25 "	15		20: 103	0	0
placed in cab-:	3		14: 4:30 "	10		20: 85	0	0
inet after	4		15: 2:45 "	5		21: 165	0	0
short period	5		17: 4:30 "	-1		18: 103	23	18
in laboratory;:	6		18: 2:15 "	-5		19: 34	133	79
temperature	8		19: 8:30 "	-14		20:	153	100
lowered gradu-:	9		25: 5:00 "	+39		27: 203	203	100
ally from 45 to -15 within 216 hrs.								
Lot 3.--Bark	Check	Jan.	18: 9:00 a.m.	48	Jan.	18: 114	4	3.3
transferred	1		18: 2:15 p.m.	19		19: 97	3	3
dir.from field:	2		: 3:20 "	14		19: 99	3	2.9
to cabinet with	3		: 4:20 "	10		20: 97	3	3
broods in dor-:	4		: 5:20 "	6		20: 98	2	2
many overwin-	5		: 6:15 "	-3		20: 71	32	31
tering condi-	6		: 9:00 "	-5		20: 11	17	60.7
tion;temp.low-:	7		19: 2:00 "	-10		20:	60	100
ered from 48	8		: 7:45 "	-15		20:	80	100
to -15 in 48 hrs.	9		20: 6:00 "	-20		21:	98	100
Lot 4.-Bark tf:	Check	Feb.	7:10:00 a.m.	60	Feb.	7: 220	4	1.7
fm.field to lab.	1		: 4:50 p.m.	20		8: 135	6	4
and kept at 60-	2		: 6:45 "	15		8: 140	4	2.5
70° for 21 days	3		: 8:10 "	10		8: 143	5	3
then tf. to	4		8: 8:50 a.m.	4		10: 125	3	2.3
freezing cab.	5		:10:20 "	0		10: 26	4	13
with larvae ac-	6		: 2:00 p.m.	-5		10: 70	93	57
tive and dev.;:	7		: 4:30 "	-7		10:	15	100
temp.lowered	8		: 9:00 "	-10		10:	70	100
fm.60 to -15° in 48 hrs.								

Table 3, concluded.

Lot.5.-Bark tf: Check*	:Feb.16:	3:30	p.m.:	26	:Feb.16:	340	: 7 :	2
fm.field to lab.	1 :	20:	11:30	a.m.:	25	:	23:	126	: 2 :	1.5
& subj.to daily	2 :	20:	1:45	p.m.:	20	:	23:	100	: 1 :	1
changes of temp.	3 :	20:	2:30	" :	15	:	23:	98	: 2 :	2
ranging fm.25-70	4 :	20:	4:30	" :	10	:	23:	105	: 0 :	0
for 6 ds.,then:	5 :	20:	8:15	p.m.:	5	:	23:	110	: 2 :	1.7
tf.to cab.& low-	6 :	21:	1:30	" :	0	:	23:	88	: 17 :	16
ered fm.70 to -15	7 :	21:	4:00	" :	-5	:	23:	46	: 75 :	62
in 48 hrs.;prel.	8 :	21:	5:30	" :	-7	:	23:	22	:120 :	85.5
variations of	9 :	21:	8:30	" :	-9	:	23:	0	:100 :	100
temp.contd.from	10 :	21:	9:40	" :	-11	:	23:	0	:100 :	100

Feb. 14 to 20

*Check removed on third day after 3 days' exposure to temperatures ranging from 26 to 74° F.

This assumption was supported in the case of other experiments with broods of the m.p.b., D. monticolae Hopk. After the larvae had been subjected to temperatures fluctuating from 20 to 50° F. for a period of several days they were observed to discharge a considerable amount of excrement from the alimentary canal. After going throughtthis process their resistance to low temperatures increased, and a high percentage of the broods survived temperatures of -15° F.

However, no tendency was observed on the part of larvae of the w.p.b. to empty the alimentary canal, and their resistance to freezing was apparently not increased by any variations of temperature preceding exposure to the fatal freezing points. In fact, Lot 5 showed a perceptible mortality somewhat higher at 5° than in the other material which was carried to subzero temperatures without preliminary fluctuations permitting short periods of activity.

Effect Upon Pupae and New Adults

Some of the material collected from Northfork was kept under laboratory temperatures until the greater part of the broods had developed to the pupal stage, and then lowered through the same range of temperatures as that containing larvae in the preceding tests. A similar test was made of another lot of material after the broods had reached the new-adult stage and were resting in the outer bark. The results from this material are summarized in Tables 4 and 5.

Table 4.--Mortality of pupae of the w.p.b. resulting from low barktemps.,1928 (Infested bark coll. at Northfork, Calif., December 1927; kept in lab. one month before freezing test was started, when about 80% of brood had tf. to pupae

Bark Sec.No.	Rem.from cabinet: Date	Hour	Bark tem.: when rem.	Date of Examination	Number of: Alive	Dead	% of Mortality
1	Mar.1:	3:00 p.m.:	26° F.	Mar.5, 1927:	94	0	0
2	1:	4:30 " :	21	" :	80	0	0
3	1:	7:15 " :	15	" :	86	0	0
4	1:	9:00 " :	11	" :	84	0	0
5	2:	8:00 a.m.:	6	" :	84	16	16
6	2:	10:00 " :	0	Feb.6, 1927:	75	27	26
7	2:	11:30 " :	-5	" :	1	99	99
8	2:	3:00 p.m.:	-8	" :	0	122	100
9	2:	4:00 " :	-10	" :	0	120	100

Table 5.--Mortality of new adults of the w.p.b. resulting from low bark temperatures, 1928. (Inf. bark coll. at Northfork, December 1927 and kept under laboratorybtmmperatures until the majority of brood had tf. to adults and were ready to emerge)

Bark Sec.No.	Rem.fm.cabinet: Date	Hour	Bark tem. when rem.	Date of Examination	No. pupae: Alive	Dead	% of Mortality
1	Mar.13	3:45 p.m.	20° F.	Mar.20,1928	90	0	0
2	"	7:00 "	13	"	82	10	12
3	"	9:00 "	10	"	7	70	90.9
4	14	7:00 a.m.	5	"	2	73	97
5	"	10;00 "	0	"	3	66	95.6
6	"	1:00 p.m.	-5	"	0	48	100
7	"	2:45 "	-10	"	0	68	100

These results indicate that pupae are somewhat less resistant to cold than larvae, as mortality was practically complete at -5° F. Adults, however, appear to be decidedly more susceptible than either larvae or pupae. High mortality results from exposure at 10° and mortality is complete at -5° F.

Effect upon Eggs in the Cambium

Difficulties not encountered with advanced brood stages in the outer bark were found in obtaining records of temperatures fatal to the egg stage. The eggs are found only in notches excavated by the parent in the cambium, and removal of the bark from the sapwood disturbs the natural conditions for incubation. Mortality due to dreezing, therefore, cannot be isolated from other factors unfavorable to incubation and development of the eggs.

Freshly-attacked logs about 8" in diameter in which parent adults were depositing eggs were selected for these tests. These were cut into blocks about 6" in length and subjected in the freezing cabinet to a range of temperatures similar to those used with the other brood stages. Temperature records of the cambium layer were secured by means of a thermometer with the bulb imbedded at this depth under the bark. After exposure the log sections were allowed to stand under laboratory temperatures of 60-75° for about ten days. The bark was then shaved from the sapwood so as to uncover the egg galleries, and a count was made of eggs which had incubated and those which had failed to develop. A characteristic bluish color distinguished the eggs that had apparently been killed as a result of freezing.

Table 6.--Mortality of eggs of w.p.b. resulting from low temps. in cambium.

Bark Sec. No.	Rem.fm.cabinet: Date	Hour	Cambium temp: when removed	Date of subsequent examination	No. eggs incubated	No. eggs failing to incubate	Percentage of mortality
1	May 23	5~~09~~ P.M.	50° F.	June 2,1928	169	9	5
2	24	9:30 am	15	"	54	3	5
3		12:00 m.	10	"	48	9	15
4		2:17 pm	5	"	45	26	36.6
5		4:30 "	0	"	51	55	51.9
6	25	2:35 "	-5	June 6,1928	22	22	50
7	26	9:45 am	-10	"	9	88	90.4
8	27	7:30 "	-15	"	11	76	87.3

It was found that the temperatures of the cambium layer within the blocks varied considerably with the moisture content and that they did not cool down uniformly, as was the case with infested bark removed from the log. Because of this factor and the limited quantity of material available, these counts do not furnish a satisfactory basis for determining the rate of mortality; however, the fact that at least 10% of the eggs incubated after they had been subjected to temperatures around -10° F. indicates that this brood stage is more resistant to cold than larvae, pupae or adults.

Effects on Larvae in Outer Bark Saturated with Water

Studies of control by the method of submerging infested logs in water at temperatures of 50 to 65°, carried on during the season of 1923, brought out the fact that larvae soon become dormant under water and remain in this condition for approximately four weeks before mortality occurs. If removed from the water and allowed to dry before this period expires, development of the larvae is resumed. In order to determine whether they lose their resistance to cold in the dormant condition produced by saturation, infested bark was soaked in water for seven days and then subjected to low temperatures. A check consisting of dry bark from the same material was run through a similar range of temperatures. The mortality at critical temperatures is shown in Table 7.

Table 7.--Mortality of larvae of the w.p.b. in saturated bark compared with dry bark when exposed to low temperatures

Bark Sec.No.	Rem.fm. cabinet: Date	Hour	Bark temp. when rem.	Date of Examination	Larvae: Alive	Dead	% of Mortality
Dry Bark							
Check	Jan.14	1:00 pm	50	Jan.14,1929	100	2	1.9
1	28	"	15	30	100	3	2.9
2	"	3:00 "	8	"	98	2	2
3	29	2:30 "	5	31	90	10	10
4	"	4:00 "	-1	"	85	15	15
5	30	2:30 "	-4	Feb. 3	55	45	45
6	31	5:05 "	-8	"		100	100
Saturated Bark							
Check	Feb.25	9:00 am	50	25	112	2	1.7
1	26	8:00 "	24	28	117	1	.8
2	"	10:30 "	20	"	104	11	9.5
3	"	12:00 m.	15	"	96	6	5.8
4	"	1:30 pm	10	"	81	22	21.3
5	"	2:30 "	5	"	60	46	43.4
6	"	4:15 "	0	"	37	98	72.6
7	27	2:45 "	-5	"	5	100	95.2
8	"	4:15 "	-8	"		100	100.

This comparison indicates a perceptible lowering of resistance to freezing as a result of saturation of the bark. This degree of saturation would occur only under special conditions, such as logs stored in mill ponds. It is obvious that the degree of saturation necessary to produce dormancy rarely if ever occurs in standing infested trees under ordinary exposure to weather.

Effect of Low Air Temperatures on Larvae Removed from Outer Bark

In addition to tests with brood stages in the outer bark, a large number of larvae wereexposed to varying temperatures in open pasteboard containers where their behavior could be observed. It was found that activity slowed down at about 50° and apparent dormancy set in between 45 and 50°. Very little change could be observed below 40° until temperatures between 15 and 10° were reached. At this point the body of the larva became rigid and took on a peculiar white color. This represents the freezing point, where the free water in the body of the insect crystallizes. If larvae are brought back from this point to temperatures of 45° or more, normal appearance and activity are resumed. However, if the temperature, instead of being raised, is lowered from the freezing point to subzero stages, mortality results and there is no recovery of activity if the insects are later brought back to temperatures above 45°. The critical temperatures established are shown in Table 8.

Table 8.--Condition and mortality of half- to full-grown larvae of the w.p.b. removed from y.p. bark and exposed to air temperatures ranging from 65 to -8° F., 1927. (Material coll. at Northfork December 1926; larvae removed from bark 2/10/27. 550 larvae were separated into 11 lots of 50 each and placed in open pasteboard containers. Temp. readings in freezing cabinet were taken with bulb of thermometer at same level as larvae in pasteboard containers.)

Lot No.	Removed from cabinet: Date	Hour	Bark tem. when Removed °F	Condition of larvae when removed	Date of examination	Number of larvae: Alive	Dead	Percent. of Mortal.
1	Feb. 11	9:10 am	65	Active	Feb. 15	50		0
2	"	10:35 "	45	Mostly active; few sluggish	"	49	1	2
3	"	11:10 "	40	Dormant	"	50		0
4	"	11:45 "	35	do	"	50		0
5	"	3:15 p.	20	do	"	50		0
6	"	4:30 "	15	do	"	50		0
7	"	5:00 "	10	do ; frozen rigid	"	50		0
8	12	12:45 "	5	do	"	41	9	18
9	15	1:05 "	0	do	18	41	9	18
10	"	3:30 "	-5	do	"	21	29	58
11	"	5:00 "	-8	do	"	0	50	100

Material was sent to Mr. William Robinson at Chicago, who determined the freezing and undercooling points of individual larvae by the special apparatus which he has devised. His records of 15 individual larvae show that the freezing point occurred from 12 to 14° above zero, while the undercooling point where mortality resulted occurred from -2 to 8°. The general effect of both high and low temperatures and the results of tests of brood stages in the bark are shown in Table 9.

Table 9.--Effect of different temps. on brood stages of the w.p.b.,1928

Temperature: °F.	Effect
120	Fatal to all brood stages after brief exposures
118,115	Complete mortality after long exposures; paralysis of lar- from which they do not recover after 20 minutes' exposure
115,110	Paralysis of larvae occursm but recovery is possible if exposure is not prolonged
110,105	Paralysis of larvae occurs after prolonged exposure; larvae recover if returned to normal temperatures
103,100	Larvae become sluggish, showing slight activity
100, 95	Activity of larvae decreases
95, 55	Maximum activity of larvae
55, 45	Activity of larvae decreases
45, 40	Larvae become sluggish and apparent dormancy sets in
40,35,20,15	Dormancy occurs in all brood stages
15,10	Larvae freeze, but recover if warmed back to active temps.
10, 5	Critical temperatures for adults; high mortality occurs at 10°; low mortality of larvae and pupae may occur at 5°
5, 0, -5,-8	Critical temperatures for larvae and pupae; mortality at 5° exceeds 50%
-8,-10,-15	Fatal to all brood stages; a low percentage of eggs and of larvae which are adapted to severe winter climates may survive these temps.
-20	Fatal to all brood stages

Effect of Low Temperatures on Parasites and Predators in the Bark

Predators and parasites of the w.p.b. were found in many of the infested bark sections used in the above tests, and observations were made as to their mortality at various points. However, this material was not sufficient in quantity to furnish a satisfactory basis for the determination of critical temperatures, although the data secured indicate that these forms differ inmtheir freezing points from the w.p.b. In the case of an undetermined chalcid parasite the temps. reached in these tests were not low enough to kill the larvae.

Effects of Low Temps. in Regions where Winter Minima Fall Below Zero F.

It is evident that in the northern limits of the distribution of the w.p.b. the winter temps. fall below the critical points indicated by the above tests. Although weather records show that minimum temps. as low as -20° F. may occur at times, at least part of the overwintering beetle population survives these cold spells. This may be due to a resistance which has been built up within the region by natural selection, or it may be due to the fact that temps. in the bark of infested trees do not reach the low points recorded by weather thermometers in the surrounding air.

Through the cooperation of Mr. J.C.Evenden of the B.E.Field Station at Coeur d'Alene, Id., where the winter climate is colder than in the y.p. belt of the Sierra Nevada region, about 25 sq.ft. of infested bark was mailed to the lab. at Stanford Univ.,Calif., and subjected to low temps. in the freezing cabinet. This bark contained broods of advanced larvae which had been in an overwintering condition for several months. During

this period minimum temps. as low as -10° F. had been recorded in the vicinity where the material was collected. Bark sections from this material were lowered from 55° to -13° with the results shown in Table 10.

Table 10.--Mortality of half- to full-grown larvae of the w.p.b. in y.p. bark subjected to temps. ranging from 55 to -18° F.; 1927. (Bark coll. at Coeur d'Alene, Id.m January 1927, with broods in overwintering condition.)

Bark Section No.	Removed from cabinet: Date	Hour	Bark Tem. when removed ° F.	Date of examination	Number of larvae: Alive	Dead	Percentage of Mortality
1	Jan. 29	12:00 m.	25	Feb. 2	112		0
2	"	4:00 p.m.	4	"	61	12	16.4
3	"	5:00 "	0	Jan. 31	119	0	0
4	"	7:00 "	-5	Feb. 1	25	23	49
5	"	8:50 "	-10	Jan. 31	25	81	76
6	"	11:00 "	-12	Feb. 1	7	56	89
7	Feb. 1	8:00 a.m.	-18	" 2	11	207	94.9
8	"	10:25 "	-18	" 2		67	100

The mortality found in Sec. 2 cannot be explained by temps. to which larvae were subjected in this test. It may have resulted from conditions in the field or in transit for which records are not available.

Although partial mortality appeared within the same range of critical temps. as in the material from Northfork, the striking difference is in the degree of survival after -5° F. had been reached. This amounted to 24% survival at -10° and 11% survival at -12°. Apparently these broods had developed a partial resistance to temps. which were 100% fatal to broods that had overwintered under warmer climatic conditions. However, this resistance was not sufficient to withstand more than 10° below the temps. which were fatal to the material collected at Northfork.

Difference Between Air and Bark Temperatures in the Field

The fact that broods of the w.p.b. do survive where weather records show minimum air temps. below those which were found to be fatal in the bark, indicates that the infested bark on standing trees does not become as cold as the surrounding atmosphere and therefore does not cool down to the critical points. This seems apparent, as the infested bark is in contact with the moist sapwood of the tree, which in turn connects with the root system in the soil. This position gives contact to a reserve of accumulated warmth which prevents rapid cooling of the bark. It would appear that only prolonged periods of subzero temps. can chill the bark sufficiently to produce temps. fatal to the broods.

Two series of records secured by J.C. Evenden and H.J. Rust support this assumption. In January 1927 and again in January 1928 periods of subzero weather occurred at Coeur d'Alene, Id. During these cold spells weather thermometers were placed in the bark on the north and south sides of an infested standing tree. At the same time thermometers were suspended in the air on the north, south, east and west sides of the tree. Readings were taken hourly during a period of 28 hours. The lowest point recorded in the readings of air temps. was -6° F., when the corresponding bark temps.

were 4 and 8° F. This shows a difference of 10 and 12° between air and bark temps. As the air temps. rose this difference decreased, and both air and bark temps. corresponded closely at 12° F. No appreciable mortality occurred in the broods, which would be expected, since critical temps. were not reached in the bark.

Further records of the comparative air and bark temps. and a study of the effects of extreme low temps. in the field are necessary before it will be possible to determine the expectancy of mortality to broods of the w.p.b. as a result of winter freezing.

Summary

1. Fatal temps. are of importance in both the artificial and natural control of the w.p.b. (D.brevicomis Lec.). Temps. in the bark high enough to result in mortality are essential in the use of the solar-heat method of control. Low temperatures in the field which result in the death of the broods from freezing may materially reduce the beetle population in infested areas.

2. High and low temps. affecting brood stages of the w.p.b. while in the bark must reach the insects through the protective covering of the outer bark. Critical environmental temps. must therefore occur in the outer bark.

3. When infested bark is removed from the log and placed where it is exposed to sunlight during the midday period, it will reach temps. ranging from 110 to 130° F. when the corresponding air temp. ranges from 80 to 95° F. A partial mortality of the broods will result if bark temps. range from 100 to 115° daily for a period of several days. Complete mortality is assured if bark temps. reach 115 to 118° for a period of 2 hours or more. No broods survive a brief exposure if the bark reaches a maximum of 120°.

4. When larvae are removed from the outer bark and exposed to warm air under conditions which retard evaporation, mortality occurs at about the same points of temp. as in the bark. If rapid evaporation is permitted, paralysis and mortality occur at points about 5° lower than in the bark.

5. Mortality of the larvae following freezing results when bark temps. are lowered below zero F. Partial mortality occurs at zero in broods which overwinter in the y.p. belt of the Sierra Nevada region; mortality at -5° exceeds 60%, and no larvae survive at -10. Temps. within the range, from zero to -10 are consistently critical, regardless of the rate at which the temp. of the bark is lowered or warmed back from subzero to normal temps.;,complete mortality develops within this range regardless of whether the larvae are actively developing or dormant at the time the bark temp, is lowered to the critical points.

6. High mortality of the pupae occurs between 5 and -5 and is complete at -8.

7. High mortality of the adults occurs between 12 and 5 and is complete at zero.

8. Tests to determine mortality of eggs were unsatisfactory and much less conclusive than for other stages of development. Results available indicate that partial mortality of eggs in the cambium occurs at temps. between 5 and -10. The mortality recorded at -15 was around 90%, indicating that eggs have greater resistance to cold than other brood stages.

9. When larvae become dormant through saturation of the bark with water they are less resistant to cold, and about 20% mortality occurs at 10. Complete mortality, however, does not occur until points between -5 and -10 are reached.

10. When larvae are removed from the bark and exposed to cold air, complete mortality occurs between 5 and -8. The point at which larvae freeze but recover if warmed back to active temps. occurs between 10 and 15. Larvae become dormant at about 45 and show no further change until the freezing point is reached. Maximum activity and development of larvae occur between 55 and 90.

11. Broods which overwinter in regions where minimum winter temps. are below zero apparently develop greater resistance to cold than in regions withmmild winter climates. Larvae which had passed through the overwintering condition at Coeur d'Alene, Id., where air temps. of -10 had been recorded, developed high mortality when bark temps. were reduced through the range from zero to -10. However, about 25% survived -10. Mortality was practically complete at -18. The difference in resistance to cold developed by regional conditions apparently does not exceed 10° of temp.

12. The outer bark on standing infested trees cools down much more slowly than the surrounding air, and does not reach the minimum temps. recorded by weather thermometers. Records obtained at Coeur d'Alene during two periods of subzero weather indicate that minimum bark temps. are 10-12° higher than minimum air temps. Further records are needed to correlate this difference between bark and air temps. to determine the probability of winter killing in infested areas.

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